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THE ORIGIN OF MONOCOTYLEDONY

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 187

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(WITH PLATES XXVIII AND XXIX AND TWO FIGURES)

The origin of Monocotyledons from the Archichlamydeae seems well enough established to need no discussion in this connection. The evidence of vascular anatomy, supported by the historical record, as well as by general morphological considerations, seems to be explicit. It remained to obtain evidence of the transition from dicotyledony to monocotyledony. This seemed to be a peculiarly difficult situation, for it appeared to involve much more than the number of cotyledons. The difference in number was disposed of in two ways, the monocotyledonous condition being said to have arisen either by a fusion of the two cotyledons or by a suppression of one of them. Each of these views can be supported by a considerable body of evidence, based upon vascular anatomy and upon many intermediate stages in fusion or in elimination. The real difficulty in the situation, however, appeared to be in the fact that in Monocotyledons the cotyledon is a terminal structure, and in Dicotyledons the cotyledons are lateral structures. How could the terminal cell of a filamentous proembryo which had been producing a stem tip change its function and persistently produce a cotyledon? Any comparison of the proembryos of *Capsella* and *Alisma*, the two accepted types of Dicotyledons and Monocotyledons, emphasizes this difficulty.

A clue to this problem was furnished by the seedlings of *Cyrtanthus*, a South African genus of Amaryllidaceae, which was investigated by Miss FARRELL,[1] a graduate student of this department. In accordance with this suggestion, seeds of numerous Monocotyledons were obtained from South Africa and Australia, These were germinated and an abundance of material obtained for study.

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[1] FARRELL, MARGARET E., Ovary and embryo of *Cyrtanthus sanguineus*. BOT. GAZ. 57:428–436. *pl. 24. figs. 3.* 1914.

The first case to attract our attention was that of *Agapanthus umbellatus* L'Hér., one of the South African Liliaceae. Although ordinarily monocotyledonous, a seedling was found with two well developed cotyledons. This discovery led us to hope that it might be used in determining the relation between monocotyledony and dicotyledony. The two conditions shown by the seedlings of *Agapanthus* are illustrated in fig. 1. If the seedlings of the same species are thus indifferently monocotyledonous or dicotyledonous, there must be some evident relationship between the two conditions.

In the following account no attempt will be made to cite the literature of the subject. It is sufficiently well known to students of Angiosperms, and most of it is available in COULTER and CHAMBERLAIN'S *Morphology of Angiosperms*. When the remaining material that has become available is investigated, a more detailed account of the whole subject of the development of cotyledons will be given.

The structure of the monocotyledonous seedling of *Agapanthus*, a photograph of which is reproduced in fig. 1, is shown by the series of transverse sections given in figs. 2–13, and by their diagrammatic reconstruction in fig. 14. The section through the cotyledon and first leaf above the cotyledonary sheath (fig. 2) shows three vascular strands in the cotyledon, arranged in a triangle, with the xylem directed toward the center. If the middle strand had not been laid down, the two laterals would show the inverse orientation that has suggested that the monocotyledonous condition has arisen by a fusion of two cotyledons. The cotyledon above the sheath is cylindrical, but as the sheath is approached it begins to invest the first leaf (fig. 3). Soon the sheath becomes a complete ring in transverse section, which increases in thickness around the leaf as the transition region is approached, until, at the junction with the first leaf, the investing sheath becomes of almost uniform thickness (fig. 9), that is, the side of the sheath away from the cotyledon is as thick as the side which is continuous with the cotyledon. In all the many seedlings sectioned, the cotyledonary sheath is a simple ring in transverse section, without any infoldings.

The three strands retain their positions with reference to one another until just above the transition region, where they approach one another, and their phloem strands become united (fig. 9). Farther down the three cotyledonary strands unite completely, and the phloem divides (fig. 10). The single bundle of the first leaf turns inward (figs. 9 and 10) and unites with the cotyledonary strands (fig. 11). The lateral bundles of the leaf are disregarded since they appear late, and in early seedling stages are not connected with the main strand or with the cotyledonary plate. This union of strands, three from the cotyledon and one from the first leaf, forms a siphonostele (fig. 11), which is the "cotyledonary plate." The strand from the first leaf continues into the hypocotyl and becomes one of the poles of the root, and from the cotyledonary strands that enter into the structure of the cotyledonary plate, two other strands pass down the hypocotyl to form poles of the root,

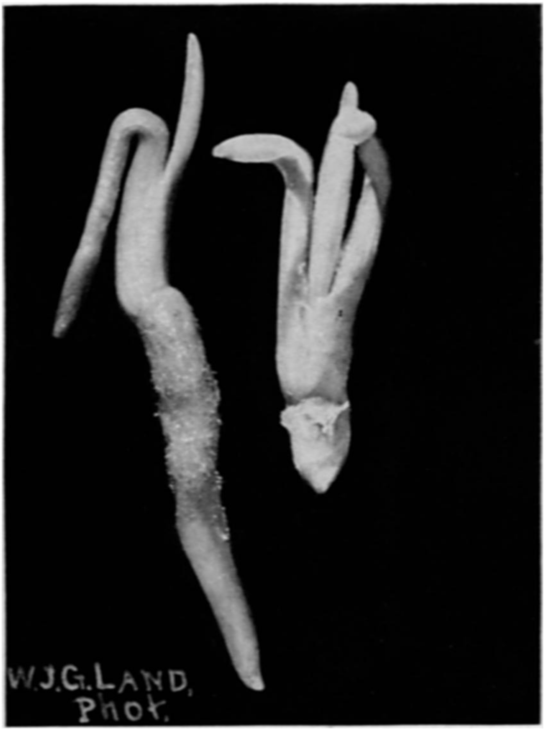


FIG. 1.—Monocotyledonous and dicotyledonous embryos of *Agapanthus umbellatus*; ×4.

which is therefore triarch. Farther down, the strand which has come from the first leaf forks, and the root becomes tetrarch. Older seedlings were not examined, but probably further forking of strands occurs, making the root eventually polyarch.

In thus describing the course of the vascular strands, the sequence given seems to be that of their formation, although we did not observe the procambial strands. If this be true, they are laid down first in the growing cotyledon and first leaf, become united later in the cotyledonary plate, which then gives rise to the root poles. This means that the vascular strands do not determine the development of the structures of the seedling, but that the primordia of cotyledon and first leaf start and the vascular strands are laid down in the growing organs. In other words, growing primordia determine the vascular strands rather than the reverse. If the cotyledonary sheath is very massive, vascular bundles may be laid down, and these may have no connection with other bundles. In the cotyledonary sheath of *Doryanthes Palmeri*, which is very thick, a vascular strand was found at a point opposite the massive cotyledon. This solitary strand had no connection with the cotyledonary plate, or with any other strand, beginning and ending blindly in the sheath. The inference seems evident that vascular strands are secondary structures, whose appearance is dependent upon the character of the primary structure, and therefore of no phylogenetic significance in the seedling.

It is noteworthy also that in the seedling of *Agapanthus* there is no stem primordium. In fact, the stem is a very belated organ, not having appeared in the seedlings under investigation. When and how a stem primordium is organized later was not seen. Certainly in the well developed seedlings of *Agapanthus* there is no stem primordium that gives rise to lateral leaf primordia. All of the meristematic tissue is involved in cotyledon and leaf-formation.

The structure of the dicotyledonous seedling of *Agapanthus* shown in fig. 1 is indicated by the series of transverse sections given in figs. 15–28, and by their diagrammatic reconstruction in fig. 29. The seedling is of the same age as the monocotyledonous one. The two cotyledons are the same length, but one is slightly thicker than the other (figs. 15 and 16). The cotyledonary sheath extends farther upward on the side opposite the first leaf, giving the seedling a slight asymmetry (fig. 17), but soon the sheath becomes a symmetrical ring in transverse section (figs. 18 and 19). Each cotyledon has two lateral strands, as if the middle one present in the monocotyledonous seedling has not been laid down. The second leaf is also well developed, so that six strands approach the cotyledonary plate (figs. 21–23). These gradually converge, the phloem of the cotyledonary strands uniting with that of the first leaf (fig. 23), and lower down with that of the second leaf (figs. 24 and 25), but the xylem does not fuse until farther down (fig. 26). As in the monocotyledonous seedling, the cotyledonary plate is a siphonostele, and the strand of the first leaf continues directly as one of the poles of the triarch root, and lower down divides, resulting in a tetrarch root.

So far as the vascular strands are concerned, the two seedlings differ in the number laid down in the cotyledons. The larger single cotyledon contains three strands, while each of the smaller cotyledons of the dicotyledonous seedling contains two strands. The organization of the cotyledonary plate and of the root poles is the same in both cases.

It is obvious that this difference in the number of vascular strands does not determine the development of one or two cotyledons; the number of strands is simply a result of the development of one or two cotyledons; for vascular strands are differentiated in the tissues of a growing organ. It seems clear, therefore, that the appearance of one or two persistently growing points in the cotyledonary region of the proembryo determines the monocotyledonous or dicotyledonous condition; and that in *Agapanthus* the number of such growing points is variable.

In comparing the two seedlings, a suspicion might arise that the so-called dicotyledonous seedling, with its two leaves as well as its two cotyledons, is a case of the fusion of two embryos, or rather two produced by a single proembryo. This possibility has not been traced through in detail, but the vascular situation just described shows that the dicotyledonous seedling is merely a slight modification of the monocotyledonous one, and gives no suggestion of the "fusion" of two embryos.

It seems evident that the variability in the number of cotyledons could appear only in massive proembryos. The conception of monocotyledonous and dicotyledonous embryos has become a somewhat rigid one because it has been based upon such proembryos as those of *Alisma* and *Capsella* as types. It has become customary to regard these filamentous proembryos as primitive and typical of the two groups, and the massive proembryos that occur in both Monocotyledons and Dicotyledons as modifications. It is our belief that massive proembryos represent the primitive condition of proembryos in Angiosperms, and that only from such a proembryo could the monocotyledonous and dicotyledonous conditions have differentiated. After this differentiation, the difference has become relatively fixed by the reduction of proembryos to filaments. While massive proembryos occur in all the three great divisions of Angiosperms, they are notably present among the Ranales, from which the monocotyledonous branch seems to have arisen; and they are also retained by many of the Monocotyledons, notably the Arales and Liliales, and in these groups one may expect to find occasional dicotyledony or even polycotyledony.

The sequence of events in the development of the embryo of *Agapanthus* is as follows. As the massive proembryo enlarges, the root end elongates, thus remaining narrow and pointed; while the shoot end widens, becoming relatively broad and flattish. At this broad and flat end the peripheral cells remain more actively meristematic than do the central cells. It is this peripheral meristematic zone that is the cotyledonary zone. In this zone two more active points or primordia appear and begin to develop. Soon the whole zone is involved in more rapid growth, resulting in a ring or tube, but with the primordia still evident. The sequence of these two stages must be kept distinctly in mind, namely, (1) the appearance of primordia, and (2) zonation. The cotyledonary zone continues its growth until a tube of considerable length is developed, leaving the apex of the proembryo depressed. In the case of the dicotyledonous embryo of *Agapanthus* the two primordia on the rim of the tube continue to develop equally, the growth of the whole cotyledonary zone being shared equally by the two cotyledons. In the case of the monocotyledonous embryos, the cells of one of the cotyledons gradually lose their meristematic activity, but those of the other one continue division, and as a result the so-called single cotyledon is developed, which is really the growth of the whole cotyledonary zone under the guidance of a single growing point. One cotyledon is not eliminated, but the whole growth is diverted into one cotyledon. Of course "tube" or "sheath" and "cotyledon" are all one structure, arising from the cotyledonary zone. As a result of the checked growth of one of the cotyledonary primordia, there soon develops the appearance of an "open sheath" and a "terminal" cotyledon. The developmental stages in this case, therefore, are first two cotyledons, and then, because of one-sided growth, one large cotyledon and one so small as to be easily overlooked.

The two primordia appearing upon the cotyledonary zone mark the places where vascular strands will be laid down. It would seem that the positions of vascular strands in such a case, therefore, are of no significance beyond indicating possibly the places where primordia have appeared, and also sometimes suggesting the number of primordia; but they cannot be used even for these purposes with absolute certainty.

It would be interesting to assemble the many cases of unequal cotyledons and note the variation in the checked growth of one of them, so that it ranges in appearance from a mere protuberance or ligule-like appendage, to a fairly well developed, but smaller, cotyledon. Such a series can be observed among the so-called pseudo-Monocotyledons. In such a series it would be noted also that if the checked growth of one of the cotyledons is very early, it will contain no vascular bundles, all the cotyledonary strands being laid down in the growing cotyledon. In many cases, as in *Cyrtanthus*, as growth is diverted from one cotyledon to the other, the procambium strands are also diverted toward the larger and later functioning cotyledon, and finally the strands unite. This phenomenon of fusing strands has been interpreted as an evidence of the fusion of cotyledons. In *Fourcroya Bedinghausii*, however, we found that the procambium strands of the primordium which represents a second cotyledon do not drift across and unite with the strands of the single functioning cotyledon. In these cases, therefore, one cotyledon is developed whether opposing strands unite or not. In monocotyledony, therefore, as shown by *Agapanthus*, the number of vascular strands in the single cotyledon is likely to be greater than it would have been if both cotyledons had developed, for the cotyledon itself is larger. It is such cases that have suggested that monocotyledony has arisen by the suppression of one cotyledon. It is not so much the suppression of one cotyledon, as the growth of the whole cotyledonary zone to form a single cotyledon. In other words, in such a case a cotyledon is no more suppressed than are petals in Sympetalae.

A further examination of the proembryos of *Cyrtanthus sanguineus*, reported upon by Miss FARRELL (*loc. cit.*), shows that in this species four primordia may appear upon the cotyledonary zone, which for a time develop equally. Then the whole zone becomes involved in the more rapid growth, giving rise to the cotyledonary ring or sheath, but with the four growing points still prominent. In the next stage the cells of the ring between a pair of growing points on each side become more active, and the four original growing points begin to "grow together" in pairs, so that two cotyledons, each with two points, begin to appear. During this stage, which may be called figuratively a "fusion in pairs," the cotyledonary sheath still continues to elongate. Later on one of the two cotyledons begins to develop faster than the other, resulting in two unequal cotyledons, which are connected at base by the thick ring. Gradually the cells of the smaller cotyledon cease dividing, and, those of the other continuing to divide, the result is a seemingly single terminal cotyledon. The developmental stages in this case are four cotyledons, two cotyledons, and finally one large cotyledon, associated with another one so small as to escape ordinary observation. The suggestion here of the possibility of polycotyledony in *Cyrtanthus* is plain, and the explanation of the polycotyledonous condition among certain Gymnosperms seems evident.

In the current accounts of the embryogeny of *Sagittaria* and of other forms with filamentous proembryos, the development of the proembryo from the filamentous condition to the organization of growing points has not been traced, and the general conclusion has been reached that the terminal cell forms the single cotyledon. An examination of the stages between the filamentous proembryo and the apparently terminal cotyledon has shown that this conclusion has been taken for granted rather than tested. It is obvious that a massive proembryo is formed before growing points appear. The terminal cell of the filamentous proembryo of *Sagittaria* develops a mass of tissue whose meristematic peripheral cells develop a ringlike cotyledonary sheath, which in the growing seedling is still recognizable as an extremely narrow ring opposite the functional cotyledon. Just within this sheath, opposite the functional cotyledon, is a plate of cells, one or two cells thick, occupying the site of the second cotyledon which started as a second growing point in the cotyledonary zone. This plate merges with the base of the sheath and the first leaf, and in one instance was observed to extend upward 160 μ, and ended in two points (fig. 30). This vestigial structure may be interpreted variously, but it seems most natural to regard it as a vestige of the second cotyledon. In *Sagittaria* and *Alisma* the "growing point" of the stem has been traced to a definite plate of cells beneath the cotyledon. This plate of cells, however, is not the stem primordium, but the primordium of the first leaf. The "notch" so characteristic of these embryos is developed by the checked growth of a cotyledon primordium on one side of the cotyledonary sheath, and at the base of this notch, which is really between two cotyledon primordia, the first leaf develops.

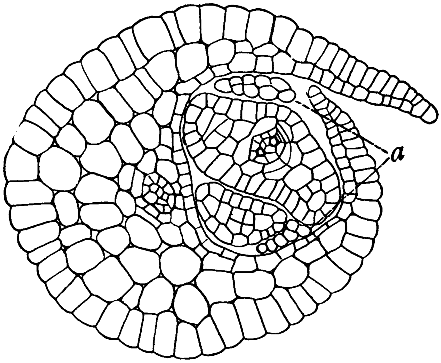
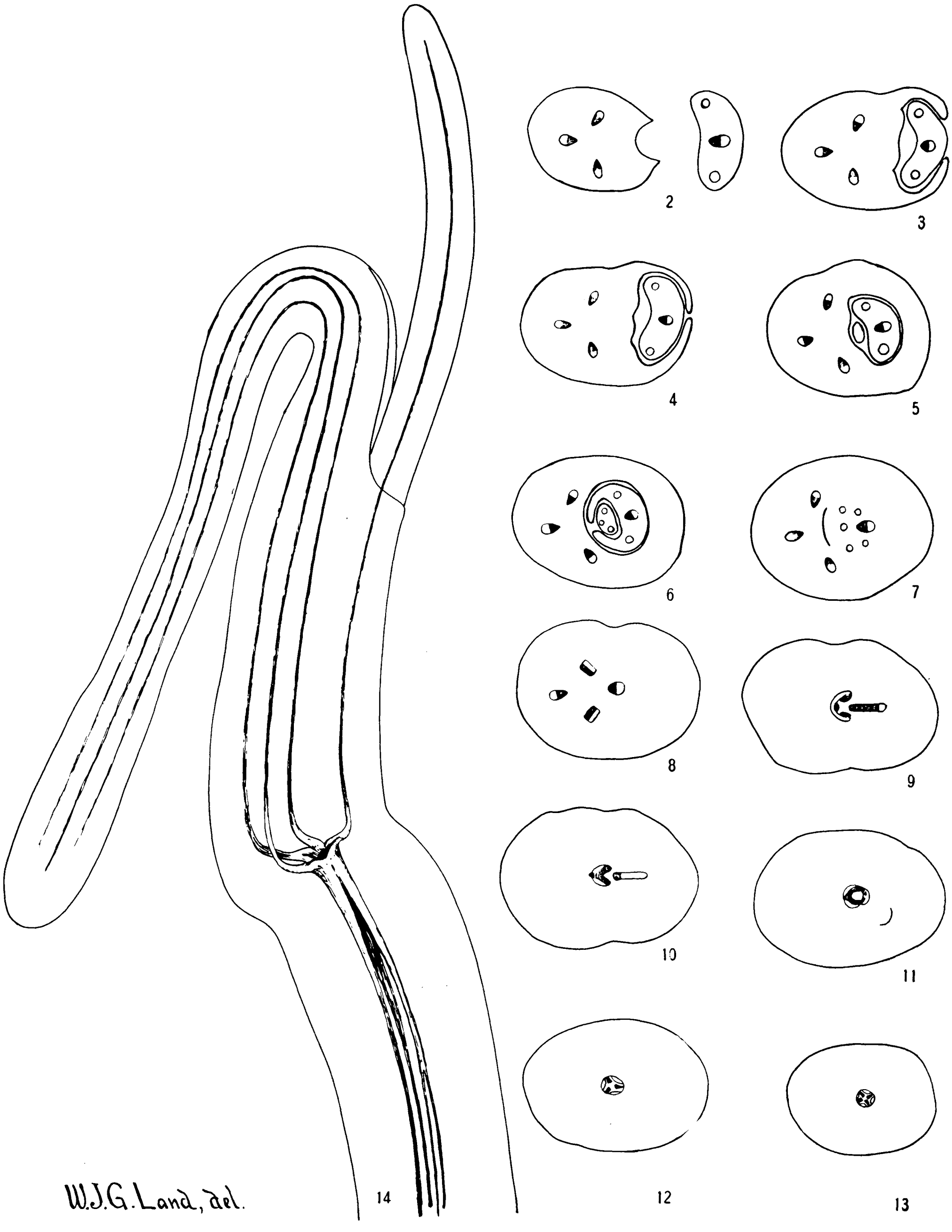


FIG. 30.—*Sagittaria variabilis:* transverse section immediately above the cotyledonary ring; *a*, rudiments of second cotyledon (?); ×150.

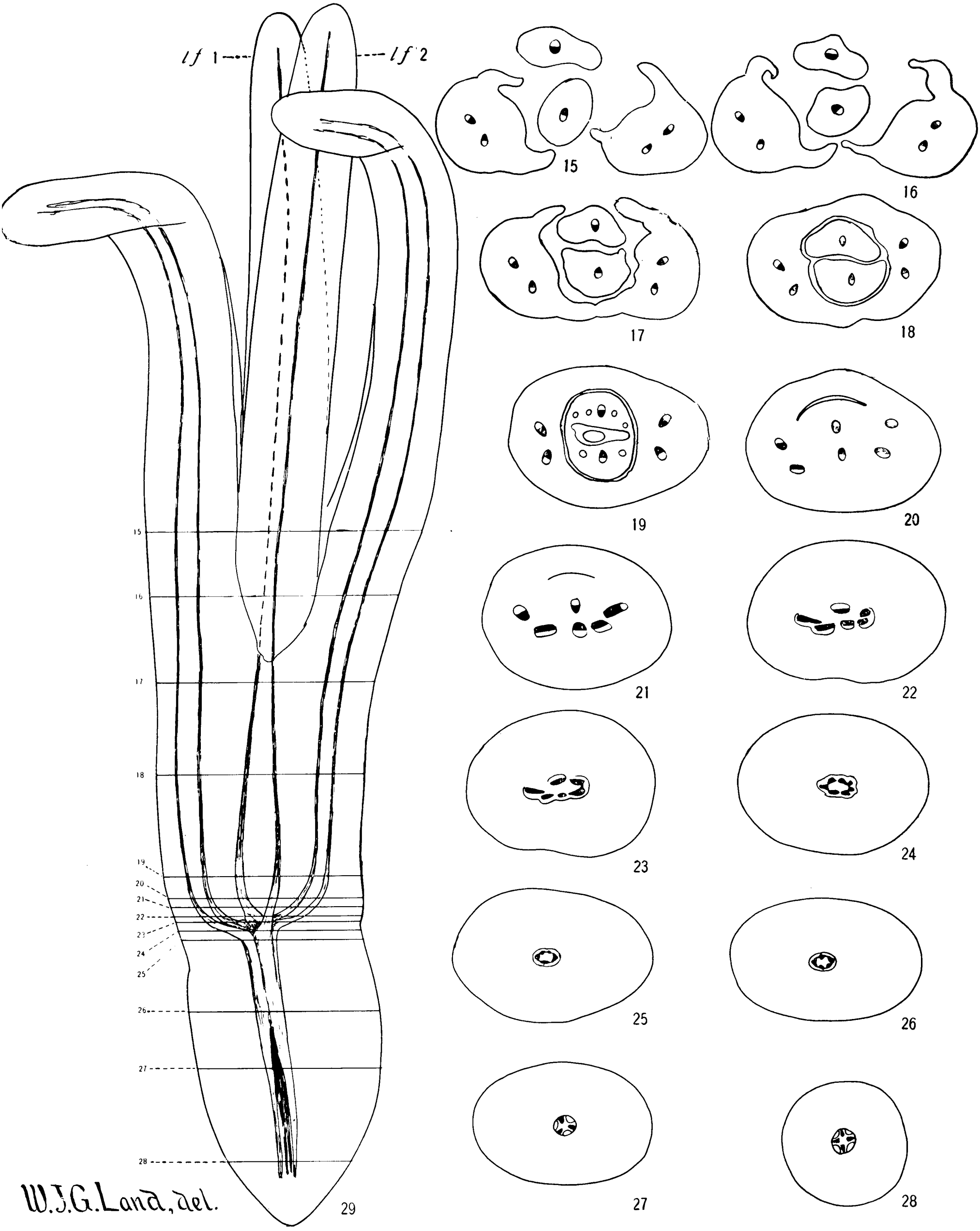
The conclusion is that in both Monocotyledons and Dicotyledons a peripheral cotyledonary zone gives rise to two or more growing points or primordia, and that this is followed by a zonal development resulting in a cotyledonary ring or sheath of varying length. If both growing points continue to develop equally, the dicotyledonous condition is reached. If one of the growing points ceases to develop, the growth of the whole cotyledonary zone is associated with that of the other growing point, and the monocotyledonous condition is reached. In other words, monocotyledony is not the result of the fusion of two cotyledons, or of the suppression of one; but it is simply the continuation of one growing point on the cotyledonary ring, rather than a division of the growth between two growing points. In the same way polycotyledony is the appearance and continued development of more than two growing points on the cotyledonary ring. In fact, in *Cyrtanthus* four growing points appear at first, which under certain conditions might result in four cotyledons. The whole situation has its parallel in sympetalous corollas, in which there is zonal development associated with three, four, or five separate growing points, which, continuing development, are recognized as petals.

It follows that cotyledons are always lateral structures arising from a peripheral cotyledonary zone at the top of a more or less massive proembryo. This reduces cotyledony in general to a common basis in origin, the number of cotyledons being a secondary feature. The constancy in the number of cotyledons in a great group is no more to be wondered at than a similar constancy in the number of petals developed by the petaliferous zone.

The organization of the stem tip in the seedling is worthy of consideration. In the mature seedlings of *Agapanthus* there is no appearance of a stem tip; all of the meristematic tissue at the tip of the proembryo is involved in the peripheral cotyledonary apparatus and the centrally placed leaves. The stem can be regarded as existing only hypothetically in the siphonostelic cotyledonary plate. Later in the history of the seedling the central region of the embryo beneath the leaves elongates and the stem structure begins to appear. If the early leaves of a plant are very small, an organized stem tip appears earlier in the history of the embryo, but it is doubtful whether in Monocotyledons any stem structure appears until late in the history of the seedling. In fact,



COULTER and LAND on AGAPANTHUS



COULTER and LAND on AGAPANTHUS

the early and vigorous development of the first leaf in Monocotyledons is probably associated with checking the growth of the adjacent cotyledonary primordium.

Incidentally the late appearance of the stem as an organized structure probably enters into the explanation of the fact that the stem is the most advanced organ of the body in structure, as vascular anatomy has indicated repeatedly. In any event, the cotyledonary strands and first leaf strands organize the cotyledonary plate, which in turn gives rise to the root poles, and later determines the character of the stem cylinder.

The main thesis of this study of cotyledony, however, is to release it from its rigid morphological categories, by showing that the cotyledonary apparatus is always the same structure, arising in the same way, and varying only in the details of its final expression.

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EXPLANATION OF PLATES XXVIII AND XXIX

FIGS. 2–14.—Monocotyledonous embryo of *Agapanthus umbellatus:* figs. 2–13, transverse sections beginning just above the cotyledonary sheath and ending in the cotyledonary plate (the sequence of numbers indicates the sequence of sections); fig. 14, a diagrammatic reconstruction of the sections; ×14.

FIGS. 15–29.—Dicotyledonous embryo of *Agapanthus umbellatus:* figs. 15–28, transverse sections beginning just above the cotyledonary sheath and ending in the cotyledonary plate (the sequence of numbers indicates the sequence of sections); fig. 29, a diagrammatic reconstruction of the sections; ×14.